

XXXVII.—*On the Mechanism of Aquatic Respiration and on the Structure of the Organs of Breathing in Invertebrate Animals.*

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[With a Plate.]

[Continued from p. 348.]

Annelida.—In the *Annelida* the function of respiration is discharged under two remarkably distinct conditions. Under the first, the chylaqueous fluid *alone* is subjected to this process; under the second, the blood-proper exclusively fulfils the office. The mechanical organs subservient to this function under the former, are constructed on a plan diametrically different from that of those provided under the latter circumstances. In the *Annelid* the true-blood and chylaqueous fluid, though coexistent in the same organism, constitute two perfectly distinct and independent fluid systems. There is between them no *direct* communication of any sort; they are *physically* very dissimilar fluids. An order of branchial processes, intermediate between the two preceding, must also be recognised, in which in equal or unequal proportions the chylaqueous fluid and the blood-proper, either in the same or in distinct appendages, participate in the process of respiration. The branchial appendages affect four different situations on the body: 1. on the head; 2. along the back; 3. along the sides, and 4. at the tail. The first rank under the *Cephalobranchiata*, the two succeeding under the *Dorsibranchiata*, the fourth are represented by the *Chymenidæ*. The *Abranchiate Annelida* resolve themselves also into two distinct divisions; those, first, which breathe through the agency of the chylaqueous fluid, and those, secondly, which expose the true blood. Both these groups would be comprehended under the *Cryptobranchiata* of Dumeril.

To these extremes, too, an intermediate order occurs; it embraces the *Nemertinidæ*, the *Liniadæ* and the *Gordiusidæ*, the cutaneous external surface of which is wonderfully and richly ciliated. In these unfamiliar genera the chylaqueous fluid and the true blood share, in unequal measure, however, the office of appropriating oxygen. Thus in succinct language has been defined "the heads" under which, in this interesting class, the mechanical conditions of respiration must be studied by the anatomist. The breathing is accomplished in every species, the *earth-worm* not excepted, in strict conformity with the *aquatic* principle. No known *Annelid* respire on the atmospheric model. In *every Annelid* the blood, though variable in colour,

is *non-corpusculated*. The converse is true of the chylaqueous fluid. No instance is known in which it does not abound in regularly and determinately organized floating cells. The physiologist recognises in these facts the presence of experimental conditions of the highest interest. When the branchial organs carry blood, perfectly devoid of morphous elements of any description whatever, yet fulfilling the purposes of breathing, the floating cells of the fluids are shown to be *not necessary* to the interchange of the gaseous elements concerned in this vital process. On the basis of these unequivocal and visible facts, it is not rash to erect the rule that the floating corpuscles of the organic fluids enact *no share whatever* in the *first* stage of the respiratory process,—that is, in that which comprehends the mere ingress of oxygen and the egress of carbonic acid; *their* office, however it may be hereafter defined, has reference to the subsequent assimilation of the oxygen with the proximate principles of the blood. Through the instrumentality of the corpuscles this quickening element is probably coerced into chemical union with the integral constituents of those principles from which a new compound eventuates.

No class of invertebrate animals unmasks so completely to the eye of the scientific observer of nature the physical machinery through which the function of breathing is fulfilled as that of the Annelida. Gifted with brightly coloured blood, every ramuscule of the blood system can be tracked to its finest extremes. Nature is more comprehensible in her humblest efforts than in her master-pieces. Her plans are susceptible of readier recognition. The intentions of the faultless Artificer are less equivocally apparent. Subtlety gives place to simplicity, obscurity to light.

The Annelids are emphatically inhabitants of the sea-shore. They are seldom afloat. Always accessible in their littoral haunts, they invite the zootomist to demonstrate in *their* organization those abstruse theorems of vital dynamics which in other beings transcend the genius of science.

The *branchial* appendages in the genus *Serpula* are grouped in erectile tufts around the head. Projecting in a comb-like form from the cephalic extremity, and tinted variously and beautifully in different species, they are admirably adapted for the exposure of the blood to the agency of the surrounding water. Each process is supported by a camerated frame or basis, large and distinct at the thick edge of the comb, from which, on one side only, projects a double row of secondary processes. This supporting framework is composed of an extremely flexible and delicate cartilage, the chambers of which are filled with a limpid fluid which is in communication with that of the peritoneal

cavity; an afferent and efferent vessel, carrying red blood, disposed in parallelism, accompany this axial framework. In the secondary processes corresponding to the teeth of the comb, the two vessels affect the inferior margin, to which the vibratile cilia are limited. These cilia are large and vigorous in action. Those of all the gills conspiring, generate a current in the surrounding water which bears in the direction of the mouth. The cilia answer therefore a double purpose: they ceaselessly renew the aërating element in contact with the branchiæ and convey food in the direction of the mouth. It is difficult to avoid contrasting the importance of *such* results with the incomplex simplicity of *such* means. Tubicolous and sedentary in their habits, the branchial appendages in the *Serpulæ* subserve thus at once the two highest functions of the organism. In this genus, *Serpula*, it is the blood-proper exclusively that is subjected to the respiratory process.

The branchiæ in the allied genus *Sabella* conform in ultimate structure with those of the *Serpulans*; they present, however, a somewhat modified disposition around the head.

In *S. unispîra* they exhibit an elegant spiral arrangement around a tapering vertical central pillar. When fully expanded, no object in nature is more beautiful: the elementary parts are comb-like; the straight processes, describing a graceful corkscrew curve around the axial stem, are multiplied by a double row of lesser filiform appendages; these latter are richly ciliated on the under surface. They carry each an afferent and efferent vessel: on the margin of extension they are strengthened by a delicate axial scaffolding of flexible cartilage. They are capable of being folded up in a small compass and withdrawn into the tube: they are extraordinarily irritable and contractile. The feet in this genus bear no branchiæ. In *Sabella à sang vert* the branchiæ rise above the head in gorgeously coloured and circularly arranged plumes: they coincide with those of the former in minute structure.

Sabella vesiculosa exhibits a slight variation of plan as compared with those of the former, in the character of the branchial processes. They are supported upon a pedunculated base: this latter is painted with spots of the gayest colours. In *Sabella à sang vert* the blood displays a deep grass-green colour; in the other species it is red. How incomprehensible such capricious freaks of nature!

The genera *Sabella* and *Serpula*, then, may be thus characterized as respects the organs and the manner of breathing. In all species the branchiæ affect a cephalic situation; the blood-proper, and not the chylaqueous fluid, is aërated; in all, the pedal appendages consist only of setæ; in all, the inferior half

of the alimentary canal is richly ciliated *internally*, a singular provision for propelling an incessant current of water from one end of the body to the other. Such a current must necessarily part at once with *its dissolved oxygen* and its suspended organic particles. The former acts upon the chylaqueous fluid contained in the *hollow* cylinder embracing the canal. This is artfully accomplished *internal* respiration!

The genus *Sabina* has been recently constituted by the author to receive several species of tubicolous Annelids which present an organization intermediate between that of *Sabella* and that of *Amphitrite*.

Sabina Poppæa expresses the generic type. The branchiæ consist of a group of short flexible processes pluming the head; they support short rudimentary secondary processes, highly ciliated; each carries a looped blood-vessel. *These* appendages aërate only the true blood: others, of a quasi-tactile character, and of unusually large size, are provided, which assume an occipital situation; they amount to three in number on either side; they are *tubular, non-ciliated*, fleshy appendages; they are penetrated by a large current of corpusculated chylaqueous fluid; they are obviously designed to oxygenize this latter fluid; they are, at the same time, subservient to purposes of touch and defence.

In *Amphitrite vel Sabella alveolata* these semi-tactile filaments, similarly situated, are considerably greater in number. Unlike those of the former genus, they are ciliated; they are hollow tubular filaments; destined to aërate the chylaqueous fluid, they communicate openly with the visceral cavity. In *A. alveolata* the true-blood branchiæ are distributed over the dorsal aspect of the body; they constitute tapering, prominent, blood-red, highly ciliated appendages carrying in their interior axially a single longitudinal blood-vessel, which at the distal extremity returns upon itself. The chylaqueous fluid also penetrates in small quantities into the interior of these processes. By M. Quatre-fages* a complex *subdivision* of the blood-vessels in these processes is figured and described. An *appearance* leading to such an error may be easily produced by pressure. A *spirally* arranged line of vibratile cilia, coiling from the base to the apex of each appendage, provides for the constant renewal of the aërating medium †.

In *Amphitrite auricoma* the branchial combs are attached by a single root, expand and divide in a pectinated manner, each tooth carrying only a single longitudinal vessel. This species

* "Organisation des Herminelles," Ann. des Sciences, 3^{me} série, 1848.

† For illustrations of many of the parts described in the text, the reader is referred to the Report of the Trans. of the Brit. Assoc. for 1851, on the British Annelida.

indicates a transition from the typical *Amphitrite* to the genus *Terebella* (fig. 1. Pl. XIV.). In all the species of the latter genus the branchial organs appear under the form of blood-red tufts (fig. 1, *a*), proceeding from three or more separate root-vessels on either side of the occiput. The vessels divide for the most part dichotomously, forming an arborescent bunch of *naked* florid branches: each ramuscle is enclosed in a delicate cuticular envelope (fig. 3, *a*²) *perfectly destitute* of cilia, and conveys to its extreme end a single vessel looping upon itself (fig. 3, *m*). Although extremely transparent and attenuated, the epidermal coating must include contractile fibres, since each branch may be emptied, rendered bloodless and shrivelled, by the compression of the parietes. This provision for reinforcing the central circulating powers exists in various parts of the blood-system of the Annelida. It may be affirmed, generally, that in all true *Terebellæ* the branchiæ occur under the character of naked, unciliated blood-vessels restricted to the occipital rings of the body. In *T. nebulosa* (fig. 1, *A*) they constitute thick, florid, resplendent tufts; in *T. conchilegia* they are fewer in number and less prominent. In the smaller species* the cephalic tentacles (fig. 2) of the *Terebellæ* constitute, unquestionably, auxiliary organs of respiration; they are copiously penetrated by the chylaqueous fluid; they carry vibratile cilia on their inferior side (fig. 2, *g*); they are capable of injection by the chylaqueous fluid; they open directly into the peritoneal chamber; they are *tubular*, flattened filaments, furnished with strong muscular parietes; they are admirably fitted to aërate the chylaqueous fluid; they are incessant in their motions; touch is obviously one of their functions; they also act as prehensile organs, conveying food to the mouth; but they are also organs of locomotion; they are fixed suctorially on a surface in advance of the animal, and used as ropes for hauling forwards the body.

In *Terebella conchilegia*, tubicolous and sedentary in its habits, the cephalic tentacles are inferior to those of *T. nebulosa* in number and size. They are differently configured; they approach the prismatic in outline; in transverse section they present a tri-radiate shape; in minute structure and mechanism of action, they differ slightly from those of the latter; they are not for locomotive purposes; hence their reduced size and diminished number.

It is not a little curious that in the *Terebellæ* these organs, which are homologous with true cirri, should be so richly provided with vibratile cilia, while the true-blood branchiæ are en-

* Several undescribed *small* species will in a future number of the 'Annals' be figured and defined.

tirely destitute of these motive appendages. Nothing but a correct conception of the nature and capabilities of the chylaqueous fluid will enable the physiologist to unriddle this apparent paradox.

The *Dorsibranchiate* order comprehends a considerable proportion of the class Annelida. "Ils ont leur organes et surtout leur branchies distribués à-peu-près également le long de tout leur corps, ou au moins de sa partie moyenne," says Cuvier. *Arenicola* represents the central genus. In this worm respiration is performed by means of naked blood-vessels projecting at the root of the setiferous processes upwards and outwards one-fourth of an inch, in the adult worm, above the plane of the surface. They are limited in number and distribution to the fourteen or sixteen middle annuli of the body. They are commonly described as forming an arborescent tuft; the division of the vessels is, however, regulated by order and symmetry. When fully injected, the vessels of each branchia form a *single* plane, rising obliquely above and across the body, and immediately behind each brush of setæ. In the adult animal each gill is composed of from twelve to sixteen primary branches, proceeding from a single trunk which arises from the great dorsal vessel: the vessels in the branchial tuft describe zigzag outlines; the secondary branches project from the salient angle of each zigzag. This mode of division, occurring in one plane and in all the smaller branches, results in a plexus of vessels of extreme beauty of pattern,—a captivating example of symmetry amid irregularity, harmony amid lawless variety. Each branchial tuft and each individual vessel possess an independent power of contraction; in the contracted state the tuft almost entirely disappears, so completely effected is the emptying of the vessels. The contraction or *systole* in any given tuft occurs at frequent but irregular intervals; this movement does not take place simultaneously in *all* the branchiæ, but at different periods in different tufts. As there exist no heart-like dilatations in the afferent vessels of the branchiæ, the contractile power with which the exposed branches are endowed, becomes an important means of reinforcing the branchial circulation. The vessels appear quite naked, and if examined in the living state, each ramuscule seems to consist only of a single trunklet; if this were really the case, it would of course resolve itself into a tube ending in a *cul-de-sac*, and the blood movement would be a flux and reflux; but by injection it is easy to show that the finest division of the branchial arbuscle contains a *double* vessel, enveloped in a common muscular though extremely diaphanous sheath. That these vascular sheaths, which are only fine productions of the integuments, are furnished with voluntary muscular fibres, is proved by the rapid

and simultaneous retraction of *all* the branchiæ into the interior of the body, which follows when the animal is touched. This sheathing of the blood-vessels with true muscular coats is a frequent character of the circulating system in the Annelida. In *Arenicola*, as in *all* Annelids in which the vessels are naked, the branchiæ are destitute of vibratile cilia.

To the frequenter of the sea-shore the preceding description of the mechanism of breathing in the familiar lug cannot prove unacceptable. Its fæcal coils are encountered at every step. The animal is ceaselessly occupied in swallowing and rejecting *wet* sand. A considerable amount of water and sand is incessantly traversing the body of the animal from one extreme to the other. The organic particles are appropriated during the digestive process; the water in part yields up its oxygen and in part replenishes the large volume of chylaqueous fluid with which the visceral cavity is distended,—another example of *internal* respiration.

Provided the branchiæ convey to the surrounding medium the blood-proper exclusively, and these organs occur in form of naked vessels projecting above the external surface, the description now given of the branchiæ of *Arenicola* will apply in every minute respect of structure to all other Annelida. It will prove exact in relation to the structure of the gills in the several species of the beautiful genus *Euphrosyne* of Savigny.

In *Euphrosyne laureata* they rise under the protection of the setæ as brightly florid brushes on the back. They are fixed by means of three or four primary trunks. Viewed by transmitted light and under a high power, each ramuscule is seen to consist of a single leafed vessel embraced in a very attenuated musculo-membranous sheath. They are destitute of ciliary epithelium.

An Annelid of great beauty of figure is described by Milne-Edwards and Audouin under the name of *Hipponoë Gaudichaudii*, in which the branchial appendages assume the character of arbuscles of naked vessels garnishing most ornately the entire dorsum of the animal. *Pleione tetrahedra*, the typical species of the genus *Amphinome*, exhibits the breathing organs under the figure of scarlet bunches mounting round dorsally each annulus of the body, and guarded in front by a bundle of strong bristles. The branchiæ in *Pleione Alcyonia* affect a ventral situation, and exhibit a much less ornamental character.

Chloeia capillata (Savigny) is an Annelid of matchless beauty. The whole line of the back on either side of the median line is decorated with arborescent vermilion tufts. Each tuft is supported by single contracted stems embracing two trunks. They are clothed with a slender musculo-cuticular *unciliated* membrane. In this rare worm the chylaqueous fluid is abundant, yet no *external* organs are furnished for subjecting it to the agency of the aërating element.

The genus *Eunice* (fig. 4) presents another and different type of branchial vessels. Arranged in a prominent row of bright vessels (*b, c, d, e, f*), standing erect as florid visible combs at the dorsal base of each foot in the body, the branchiæ impart to all the species of this genus a graceful and characteristic appearance. In every species the branchial vessels divide on a uniform plan peculiar to this genus. The primary trunk (*a*) rises vertically along the inner side of the branchia, and detaches from its outer side at regular intervals, straight vessels, which gradually decrease in size from below upwards; each branch forms a straight undividing vessel (fig. 5, *i, j*), curving gently upwards and towards the median line; these branches become *in their number* distinctive of species. In some of the smaller species inhabiting the British coasts, the branchiæ are composed only of a *single* vessel; this is the case also with the *young* of the larger species; in others they vary the single to the number of six or eight. In *Eunice gigantea*, according to the figures of Milne-Edwards, the vessels of each branchia amount to thirty-six in number. These vessels, although perfectly naked and unciliated, like those of *Arenicola*, are both less contractile and retractile; they extend in this genus from the head to the tail, and equal in number the annular segments of the body. In the dorsibranchiate genera, the branchial organs of which are now being described, the true blood circulating in its proper vessels is exclusively the seat and *subject* of oxygenation.

The fluid of the peritoneal cavity, abundant in quantity and highly organized though it be in the genera under review, does not, at least by means of any external organs, participate in this great function. Judged by such a test, the genera of this grand order of worms should be marshalled under two primary groups, of which one would comprehend those in which the function of breathing devolves *exclusively* on the true blood, while the other would be characterized by the fact, that the branchiæ are so organized as to permit separately or conjointly the exposure of the chylaqueous fluid. When the branchial apparatus is penetrated by two separate and distinct fluids, coordinate probably in organic properties, the vascular system of the body will be found in general by so much the less developed by how much the chylaqueous fluid supplants the blood-proper in the branchiæ. The *structure* of the branchial organs becomes thus a significant test of the position of any given species in the Annelidan scale—those being entitled to the highest rank of which the respiratory organs are designed to aërate the true blood, those the lowest in which the chylaqueous fluid alone circulates in the branchiæ.

The subgenera *Lysidice*, *Aglaura* and *Ænone*, of the genus *Eunice*, are distinguished in the circumstances now defined from all the former genera of the dorsibranchiate order. Naked un-

ciliated blood-vessels no longer in them form exclusively the branchial organs; loose and large-celled tissue is superadded to the proper blood-vessels, which are far less in relative size than those in the former variety of branchiæ; into the cells of this tissue the fluid of the visceral cavity insinuates itself, its course being marked by a slow flux and reflux motion. There exists, however, another point of structural difference between the branchial organs of this group and those of the former; this difference admits of the following general expression—that wherever the chylaqueous fluid is admitted into the interior of the branchial organs, the latter are invariably supplied more or less profusely with vibratile cilia.

In the genus *Lysidice* the branchia consists of a flat, lanceolate process, more or less developed, surrounded marginally by a blood-vessel, the mid-space between the lines of the advancing and returning vessels being composed of large-celled lacunose tissue, into which the chylaqueous fluid penetrates by an advancing and receding movement. The branchiæ in *L. Ninetta* are situated dorsally, and are supplied at their bases with single rows of vibratile cilia. Those of *Aglaura fulgida* are similarly constructed, although they differ slightly from those of the former genus in size and figure. In *Enone maculata* they occur under a more developed form, constituting flattened pointed trowel-shaped processes, the plane of which is vertical with reference to that of the body. A blood-vessel, as in the former case, trends along the borders, immediately beneath the cuticle. The course of these vessels is followed by a row of large and prominent vibratile cilia*.

In the branchial system of the genus *Nereis* (Cuvier), *Lycoris* (Savigny), the minute anatomist encounters a structure strikingly dissimilar from anything hitherto described in the Annelids. Whether round, or laminated, or foliaceous, the true branchiæ in this genus are always penetrated by the chylaqueous fluid, and the blood-vessels assume a peculiar disposition. When the branchial process is conical in shape, its base is embraced by a *reticulated* plexus of true blood-vessels, which are situated quite superficially and immediately beneath the epidermis. These vessels are most prominently developed on the dorsal-most process, which therefore may be called the branchial, but they extend more or less over all the cirri. A better characteristic of the branchiæ in the Nereids is that of being penetrated by the fluid of the visceral chamber. In those species in which the branchial process is conical, the interior of the base only is hollow and filled with chylaqueous fluid. Floating in this fluid may be readily

* See plates in the author's Report on the British Annelida, Trans. of Brit. Assoc. for 1851.

seen, when viewed by transmitted light, coils of naked blood-vessels; in those instances in which the branchiæ are laminated or foliaceous, as in *Nereis renalis*, the blood-plexus on the external surface does not extend beyond the limits of the base of the process, the flat, leafy circumference being tunnelled by straight spacious canals which radiate with great regularity from the root to the expanded border of the fan. In these canals the corpuscles of the chyalaqueous fluid may be observed rolling to and fro, advancing and receding in the same channel. These movements are regulated by those of the current in the chamber of the peritonæum. This type of structure prevails in *Nereis renalis*, *N. longissima*, and in a slightly modified form, in consequence of the less flattened shape of the branchiæ, in *N. viridis*. The round or conical variety of branchial process obtains in *N. margaritacea*, *N. Dumerillii*, *N. fucata*, *N. pelagica*, and *N. brevimanus*.

It is difficult to explain why the branchial organs of the Nereids should be entirely destitute of ciliary epithelium.

The laminated or foliaceous type attains the point of maximum development in the branchial appendages of the genus *Phyllodoce*. Anteriorly to the discovery of the vital and organic characters of the chyalaqueous fluid, the real uses of the rich leafy expansions ornamenting the sides of these attractive Annelids could only have been rudely conjectured. They look more like oars than branchiæ, natatory more than respiratory organs. In the absence of correct ideas tending to a knowledge of the nature and capabilities of the fluid contents of the visceral chamber, the real meaning of the radiating channels by which the respiratory laminæ are perforated, and therefore of the mechanism of the function of which they are the scene, never could have been rightly apprehended. It was only by mistaking the chyalaqueous fluid for the true blood that the branchial office of these appendages could have been predicated, and this very mistake has been committed by M. Quatrefages.

The branchiæ in *Phyllodoce viridis* are prominent dorso-lateral appendages; in this worm the blood-system can be traced only to a few scanty vessels distributed over the roots of these processes: nor are the canals very spacious and distinct; they are more like lacunæ in a spongy tissue.

In *P. bilineata* and *P. lamelligera*, radiating passages, distinct from each other and communicating only indirectly through intermediate cells, are readily observed. They carry the visceral fluid, the corpuscles of the latter being seen flowing and ebbing in the same channel. Nothing can, however, more conclusively prove the true branchial character of these laminæ than the presence of cilia, the vibrations of which can be observed only at

the edges of the respiratory laminæ: these cilia are most conspicuous in *P. lamelligera*. This is a striking point of distinction between the *Phyllodoceidæ* and the Nereids, in which ciliary epithelium has no existence. The chylaqueous fluid then may be clearly affirmed as that agent in the œconomy of the *Phyllodoceidæ* which is the immediate, *the first*, subject of the respiratory process, the true blood receiving its supply of oxygen from this fluid, afterwards to convey it to the solid structures of the body.

In the genus *Glycera* the blood-proper is entirely excluded from the organs of respiration: this office devolves exclusively on the chylaqueous fluid. The latter in this worm is crowdedly charged with *red*-corpuscles, a remarkable exception to the Annelidan rule. The gills consist of hollow, cylindrical appendages, emanating from the base of each dorsal foot at its superior aspect, filled in the interior with the chylaqueous fluid. It is peculiar to and distinctive of this genus that the *interior* of the branchiæ is lined with vibratory epithelium. Cilia are not detectible on the *exterior* of these processes, but they exist in the *interior*: under the action of these oarlets, the corpuscles of the chylaqueous fluid by which the gill-process is penetrated, move with great rapidity in a definite direction;—peripherally on one side and centrally along the other, each corpuscle whirling on its own axis as it proceeds. The advancing stream, however, is not divided from the returning. The channel is one, open channel. This is the *law* which is applied to the chylaqueous fluid: it knows no exception. *Its* channels are always single and cœcal: its movements a flux and reflux. Contrarily the orbit of the true blood is *circle*-like, its channels closed, its colour red, its composition non-morphotic.

In the *Syllidæ* (fig. 6) the branchial organs are penetrated only by the chylaqueous fluid. It can be detected only at the bases of the feet (*d*). To this part the vibratile cilia are restricted (*c*). The long filiform, and in some species moniliform or leafy appendages which are described commonly as the branchiæ in these worms, have no central hollow; they are filled with lacunose tissue (*f*) through which the *fluid* parts of the contents of the visceral chamber slowly penetrate. But in the spacious chambers occupying the bases of the feet, the *corpuscles* may be detected in whirlpools. From this fact the inference may be drawn that the corpuscles are not essential to the *first* mechanical stage in the respiratory process—that of receiving oxygen directly from without. The characters of structure just described are very perfectly typified in *S. prolifera*, the moniliform variety is best seen in *S. armillaris* and *S. maculosa*. A similar conformation prevails in the genera *Ioida* and *Psamathe* of Dr. Johnston. In the Syllidan family, which excels all others in grace and beauty,

the blood-proper system is almost undetectable, in consequence of the colourlessness of the contents. The blood does not participate in the function of breathing: it is an office performed exclusively by the chylaqueous fluid.

Amongst the family *Ariciadae* several other varieties in the configuration of the breathing organs occur. In the genera *Nerine* (fig. 8) and *Aricia* the branchial appendages affect a dorso-lateral situation: they are traversed in every species from base to apex by a single blood-vessel returning upon itself (*i*). This vessel is supported by a lobule of spongy tissue (*f*), into the cells of which the chylaqueous fluid insinuates itself. In every species of this family the branchiæ are supplied by vibratile cilia, exhibiting in each a distinct disposition. In ultimate structure, those of *Amphitrite alveolata* and *Leucodore ciliatus*, remote specifically from the Syllidans, display the same construction.

In the genus *Spio*, abundantly common on our shores, the respiratory organs occur under forms of the highest beauty. They constitute flat membranous penknife-shaped appendages curving gracefully over the back and crossing over the median line, alternating imbricatively with the corresponding processes of the other side. The plane of each process is vertical in relation to the long axis of the body (fig. 8). They are less flat and close in *N. vulgaris* than in *N. coniocephala*; they are largest in size towards the middle of the body, smallest anteriorly and posteriorly. The blood-vessels, the afferent and efferent, run close to and parallel with the inferior border of the process; the upper part of each is composed of a membranous lobular (*g, f*) addition to the inferior and vascular portion. Into the cells (*g*) of this lobule the chylaqueous fluid slowly finds its way, and participates obviously in the office of respiration. In *N. coniocephala* it is remarkable that the cilia should be limited in their distribution to the margin along which the true blood-vessel runs. This fact is manifest in *N. vulgaris* in consequence of the smallness of the membranous lobule. In *Aricia Cuvieri* the branchial appendages are more conical in figure, more vertical in position, and developed only at the posterior four-fifths of the body: they are covered with large vibratile cilia. Like those of the former, they are supplied with flat lobules of spongy tissue. In all the members of the preceding family the real branchial organ consists of an evolved or exaggerated development of the superior element of the dorsal foot.

In the genus *Nephtys* (fig. 7, A) which comes now under review, it is the inferior element of the dorsal foot which becomes the subject of this evolution. It is a curved conical process (*a*), attached to the inferior aspect of the root of the upper foot. It is hollow and filled with the chylaqueous fluid, the corpuscles of

which are readily observed on external examination (B, a). No cilia exist on the interior surface: they are abundant and vigorous on the exterior. A rich vermilion coil (*b, c*) filling the hollow of the process and *floating in the chylaqueous fluid* may be seen by transmitted light. This is a true blood-vessel: it is a single vessel. It is a law in many Annelids that the ultimate blood-vessels do not form plexuses: this proceeds from the extreme mobility of the body. The *quantity* of the blood-proper varies as the Annelidan organism varies at different seasons; it is greatest during the reproductive season, a season during which the chylaqueous fluid is most *reduced* in amount. The two fluids, though coordinate in physiological capacities, are governed by *inverse* laws.

In *Cirrhatus Lamarckii* and in the allied genus *Ophelia*, a linear series of yellowish blood-red threads, remarkably irritable and contractile, project to a considerable distance from either side of the body throughout its whole length: at the occiput they are grouped over the dorsum. They convey the blood-proper *exclusively* in a *single* vessel of considerable length.

The *Aphroditaceæ* constitute a group of Annelids to which the term dorsibranchiate by no means correctly applies; that is, in the majority of the species embraced in this order no branchial appendages exist either on the dorsum or sides. In all the *Aphroditaceæ* the blood is colourless. The blood-system is in abeyance, while that of the chylaqueous fluid is exaggerated. But it is exaggerated only in bulk; it is not raised in organic composition; its corpuscles are scanty, and its albumen small in relative amount. This unusual fact is explained by the presence of organized corpuscles in the dark chymous fluid which fills the gastric diverticula. The scales or elytra fulfil an important purpose: they rise and fall. In rising under muscular action, they create a vacuum in the space between them and the back, into which the water rushes; in falling or collapsing, the water escapes in a current posteriorly. *These currents of water operate immediately upon the fluid contained in the gastric pouches.* The latter are arranged so as most advantageously to receive the influence of the external aërating element. But they float also in the chylaqueous fluid: this is also in part oxygenized. It is the agent by which this vivifying element is conveyed to the solids of the body; it shares directly in the function of respiration; it receives its organic principles from the contents of the gastric cæca.

It cannot have escaped observation, that there prevails a striking resemblance between the general anatomy of *Aphrodita aculeata* and that of the Asteridæ among the Echinoderms. In the latter, however, the chylaqueous fluid fulfils exclusively the

office of breathing. It intervenes between the contents of the digestive cæca and the aërating element. The link of zoological continuity between the Echinoderms and the Annelids is not more clearly constituted by *Aphrodita aculeata*, than the Cestoid and Trematode Entozoa are joined to the Annelids by the transitional family of the Nemertinidæ. From the Entozoa the latter differ in the extraordinary feature of being embraced in ciliated epidermis. Every part of the external surface of the body in the Nemertinidæ is the scene of active ciliary vibration. No approach to the development of this epithelium occurs in any Entozoon. The five genera *Valencia*, *Borlasia*, *Nemertes*, *Polia cerebratulus* and *Oerstedtia*, into which M. Quatrefages has distributed the Nemertine Annelids, are exemplified on our coasts.

From the Cestoid and Trematode Entozoa several of these Annelids are distinguished by the presence of *corpuscles* in the chylaqueous fluid. In others of them the fluid conforms in character to that already defined in these parenchymatous worms. To the latter the Nemertinidæ are united by another striking peculiarity, that the cæcal *diverticula* of the alimentary system are filled with a *corpusculated* fluid, which, from the methodized distribution of these parts throughout the body, participates unquestionably in the function of respiration. The Nemertinidæ, intimate though their alliance may be with the Cestoid and Trematode Entozoa in general plan of construction, are separated from the latter in one important particular:—in the Annelids the blood system is obviously present, the blood-proper being brightly red in colour; in the Entozoa the existence of this system must for the present be held as doubtful.

It remains to consider the mode in which the process of breathing is accomplished in the *Abranchiate* Annelids, *i. e.* the leech, the earth-worm, and the Nais.

In all systematic works these worms are summarily dismissed as “breathing by the surface.” In *Nais filiformis* (fig. 10) the blood-proper is only very scantily distributed over the cutaneous surface; it is impossible therefore that *it* can be the immediate subject of the first act of aëration. The visceral chamber (*d*) in this little worm is filled with a corpusculated fluid: in this fluid coils of blood-vessels (*f, f*) are suspended. The blood-proper systematically, by expressly provided vessels, thus brought into intimate contact with the chylaqueous fluid, interchanges constituents with the latter: the former yields up to the latter its carbonic acid, and the latter to the former its oxygen. The chylaqueous fluid thus becomes to the blood-proper the aërating medium. Respiration thus explained is literally *internal*, but not the less real.

In the instance of the earth-worm the chylaqueous fluid is almost

entirely suppressed, and the visceral cavity obliterated. This vulgar worm, however, does not breathe on the atmospheric, but on the aquatic principle. It dies rapidly in perfectly dry places. Its cutaneous surface is the scene of a dense plexus of blood-proper vessels. It is always enveloped in a stratum of viscid fluid, which is remarkable for the property of absorbing and *dissolving* atmospheric air. This air, brought thus into immediate and intimate contact with the surface of the body, operates directly upon the blood-proper circulating in the cutaneous plexus. In the Abranchiate Annelids as in many of the tubicolous Annelids, the alimentary canal is profusely supplied *always* with a vascular tissue which shares in the respiratory process: this process may be distinguished as the intestinal respiration.

In the genus *Clymene* (fig. 9) the branchial organs are situated at the tail (*c*). In ultimate structure they correspond in every particular with those of the Sipunculidæ—they are *hollow* membranous projections (B) penetrated by the chylaqueous fluid (*e*) in which a coiled blood-vessel (*d*) floats. They are destitute of cilia. They afford the only illustration in the class Annelida of branchial organs specialized around the *outlet* of the alimentary system.

It has now been shown that the branchial organs in the Annelida arrange themselves under two leading divisions, between which a clearly legible line of demarcation exists. Under the one, the blood-vessel-bearing branchiæ occur; under the other, those range which are organized for the exposure of the chylaqueous fluid. Vibratile cilia are never superadded when the blood-proper alone enters the gills; *generally*, when this and the chylaqueous fluid participate in the process; *always*, when the latter alone enacts this function. The mechanism of respiration in the Annelid demonstrates beyond doubt that the agency of floating corpuscles is not required for the *absorption* of the external oxygen. The blood-proper, though coloured, is non-morphotic in *every* species. It has been proved that the tentacles are not simply organs of touch: with a single instrument nature accomplishes various ends. They are subsidiary organs of respiration. They are injected always with the chylaqueous fluid. It is certain therefore that in the œconomy of the Annelid the blood-proper and chylaqueous fluid are co-equal elements; they are convertible proximate principles; they exhibit equal physiological capacities; both are capable of discharging the function of respiration, and both are capable of supplying the solids of the body with the materials of increase.

EXPLANATION OF PLATE XIV.

- Fig. 1. (A.) Cephalic end of the body of *Terebella nebulosa*, laid open to show the afferent vessel (*d*) and efferent vessel (*e*) of the true-blood branchiæ (*a*); *c*, denotes a corpuscle of the chylaqueous fluid filling the peritoneal cavity of the body, and communicating directly with the hollow axes of the tentacular filaments (*b*).
- Fig. 2. exhibits the extreme end of one of the tentacular filaments (*b*, A) viewed by transmitted light; *f*, vibratile cilia; *g*, ditto, covering the under surface; *i*, a true-blood-vessel floating in the chylaqueous fluid, of which the corpuscles are seen rolling out at (*j*).
- Fig. 3. Extreme division of one of the true-blood branchiæ (*a*, A); *i*, afferent vessel dividing dichotomously, returning upon itself at *m*, and ending in the efferent vessel (*k*); *a*² & *n*, mark the thin, contractile envelope by which the vessels are embraced.
- Fig. 4. Foot and branchial appendage of *Eunice margaritacea*: *m*, afferent vessel entering the base (*a*) of the branchial process, of which *b*, *c*, *d*, *e*, *f*, are five vertical branches. Each branch as seen at fig. 5 consists of a single vessel (*i*) returning in a looped manner upon itself (*j*); *g*, cirrus of superior foot; *h*, inferior foot; *g*, inferior cirrus.
- Fig. 6. Foot of *Syllis* — (Williams*): *e*, cavity enclosed by the foot and filled with the chylaqueous fluid (*d*); *c*, vibratile cilia clothing the exterior; *a*, branchial process; *f*, its lacunose tissue; *e*, exterior cilia.
- Fig. 7. (A.) Foot of *Nephtys Hombergii*: *a*, branchial process, depending in form of cirrus from the base of the superior foot: (B.) an enlarged view of the branchial process examined as a transparent object. It consists of a hollow process filled with the chylaqueous fluid, in the midst of which is seen floating a long, undividing, complexly coiled true-blood-vessel (*c*). The process is lined externally by a ciliated epithelium.
- Fig. 8. Vertical view of the foot of *Nerine vulgaris*: *k*, cavity enclosed by the base; *m*, corpuscles of the chylaqueous fluid by which it is filled; *h*, *f*, *g*, channels penetrated by the chylaqueous fluid in the fleshy lobules; *i*, true-blood-vessel occupying the hollow of the process; *c*, *d*, flat cirri of the upper and lower feet; *o*, cilia; *a*, *b*, integuments.
- Fig. 9. *Clymene Ebiensis*: *a*, mouth; *b*, first row of hooked setæ; *c*, branchiæ projecting from the tail; B, one frill of the branchial process detached and viewed transparently; *e*, *f*, corpuscles of chylaqueous fluid by which the lobules are filled; *d*, true-blood-vessel floating in the fluid.
- Fig. 10. A part of the mid-body of *Nais filiformis* viewed by transmitted light—showing the same precise relation between the chylaqueous fluid (*e*) and the true-blood-vessels (*f*, *f*) as exists in the branchiæ—proving that although the parts are internal, the conditions of respiration are complete: *a*, intestine; *b*, *c*, dorsal and ventral primary vessels; *d*, cavity of the body.

* This species will be described in a future number of the 'Annals.'